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Cestoda from Lake Fishes in Wisconsin: The Ecology and Interspecific Relationships of Bothriocephalid Cestodes in Walleye, *Stizostedion vitreum*

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ABSTRACT: A total of 1,812 fishes of 32 species from Silver Lake (Kenosha County) and Tichigan Lake (Racine County), southeast Wisconsin, and 1,543 fishes of 27 species from connected waters, were examined for parasites. Only walleye, *Stizostedion vitreum,* from Silver Lake were infected with both *Bothriocephalus formosus* (a new host record) and *B. cuspidatus.* Green sunfish, *Lepomis cyanellus,* from Tichigan Lake canal were also infected with *B. formosus.* The description of *B. formosus* is addended from autumn and spring collections. Available museum specimens were examined critically and some were reidentified. The relationship between growth and development of *B. formosus* was related to season (temperaturee) and host species. *Bothriocephalus formosus* was more dominant than *B. cuspidatus.* It was present in walleye all year, but its major recruitment and reproductive seasons were autumn and summer, respectively. *Bothriocephalus cuspidatus,* which competed with *B. formosus* for pyloric ceca, was absent from walleye during summer when *B. formosus* reached its peak intensity of infection and reproductive activity. Peak reproductive season of *B. cuspidatus* was in the autumn. This is considered to be a case of temporal segregation of reproductive niches. Prevalence and intensity of infection of both *Bothriocephalus* species did not appear to be related to host size or sex. *Pomoxis annularis, P. nigromaculatus, S. vitreum, Micropterus salmoides,* and *Ambloplitis rupestris* appear to be paratenic hosts of *Bothriocephalus* in Silver Lake; the first to be reported.

KEY WORDS: cestodes, Wisconsin, *Bothriocephalus, Stizostedion vitreum,* morphology, ecology, interspecific relationships, seasonality, host size and sex, site selection.

This report addresses various ecological relationships between 2 species, *Bothriocephalus formosus* Mueller and Van Cleave, 1932, and *Bothriocephalus cuspidatus* Cooper, 1917, infecting walleye, *Stizostedion vitreum,* from 2 eutrophic lakes in southeast Wisconsin. Early studies of fish parasites in various Wisconsin waters included parsite–host lists, which were occasionally annotated. Both species of cestodes were previously reported in western Wisconsin (Fischthal, 1947; Kuntz and Font, 1984), but *B. cuspidatus* was more widespread elsewhere in northern and eastern Wisconsin and in other Great Lakes states (see Hoffman, 1967). The fact that both species of cestodes utilized the same fish species as the definitive host in this study provided a unique opportunity to study their interspecific associations, habitat occupancy, host relationships, and variations in their temporal pattern of reproduction. Morphological comparisons and ecological information contained herein are reported in the North American literature for the first time.

Materials and Methods

Walleye were examined from Silver Lake (Kenosha County), a 188-ha eutrophic land-locked lake, and Tichigan Lake (Racine County), a 458-ha lake in an advanced state of eutrophication on the Fox River (tributary of the Mississippi River). Seasonal biweekly collections were made from both lakes during spring (April), summer (June, July, and early August), and autumn (late October and November) between 1977 and 1979 and also from Silver Lake during the summer of 1976.

Fish were electro-shocked and dissected shortly after capture. The stomach (region A), the first and second loops of the small intestine (B_1 and B_2) and the first and second halves of the large intestine (C_1 and C_2) were systematically examined for parasites. Cestodes were fixed, stained, and mounted as in Amin (1986a) and categorized as juveniles (strobila with no or only immature proglottids), mature adults (posterior proglottids sexually mature), and gravid (at least some proglottids with eggs). Mean refers to the number of worms recovered/number of fish examined, and prevalence is the number of fish infected/number examined × 100. Representative specimens were deposited in the U.S. National Museum Helminthological Collection (USNM Helm. Coll.) and in the University of Nebraska State Museum Harold W. Manter Laboratory Collection (HWML Coll.).

Results

Only walley from Silver Lake were found infected with either species of cestodes.

Variability

The morphometrics of *B. formosus* from walleye in Wisconsin were similar in the autumn and

Table 1. **Comparison between major anatomical features of *Bothriocephalus formosus* from Wisconsin and the type material.***

Character	Wisconsin material: Autumn/spring $N = 8$	Wisconsin material: Summer $N = 11$	Type material: Mueller and Van Cleave (1932) description	Type material: USNM Helm. Coll. No. 8690 cotypes $N = 6$
Strobilar length (mm)	102.50 (74.00–130.00)†	29.50 (18.00–38.00)	Rarely exceeding 30	27.15 (21.20–34.00)
Max. width (mm)	2.06 (1.60–2.44)	1.11 (0.84–1.37)	1.3	1.05 (1.00–1.12)
Scolex length (mm)	1.16 (1.12–1.26)	0.83 (0.70–0.98)	0.32–0.475	0.46 (0.42–0.49)
Max. width (mm)	0.45 (0.36–0.52)	0.37 (0.27–0.42)	0.13–0.23	0.20 (0.14–0.25)
Neck width (mm)	0.27 (0.22–0.31)	0.18 (0.15–0.31)	Similar to scolex width	0.16 (0.14–0.17)
Mature seg. length (mm)	0.60 (0.36–0.76)	0.40 (0.28–0.49)	0.4–0.6	0.54 (0.40–0.60)
Width (mm)	2.00 (1.37–2.44)	0.88 (0.71–1.09)	0.8–1.2	0.97 (0.88–1.12)
Gravid seg. length (mm)	0.97 (0.72–1.20)	0.53 (0.42–0.63)	—	0.69 (0.60–0.84)
Width (mm)	1.95 (1.60–2.44)	1.11 (0.84–1.37)	1.3	1.03 (0.92–1.12)
No. of segments	380.2 (277–443)	119.9 (81–158)	—	105.7 (92–120)
% gravid	10.7 (8.0–16.0)	17.7 (8.0–30.0)	—	14.5 (6.0–27.0)
Testis dimensions (μm)	120 (106–134) × 110 (80–128)	89 (76–109) × 76 (61–99)	—	81 (70–112) × 68 (58–90)
No.	50.7 (45–58)	44.1 (34–60)	30–45	41.5 (32–55)‡
Cirrus sac dimensions (μm)	285 (238–350) × 251 (196–336)	204 (154–238) × 186 (140–238)	—	151 (115–196) × 132 (96–154)§
Ovary width (μm)	630 (490–728)	399 (294–560)	—	274 (238–322)
Egg length (μm)	55 (48–64)	53 (48–64)	53–59	56 (51–61)
Width (μm)	39 (32–45)	38 (32–48)	33–35	41 (38–48)
Vitellaria dimensions (μm)	69 (48–83) × 54 (42–64)	54 (38–64) × 44 (35–51)	—	42 (32–51) × 33 (26–42)

* All the Wisconsin specimens and the cotypes were gravid.

† Mean (range). Two testes, cirrus sacs, ovaries, eggs, and vitelline glands were measured and/or counted in each cestode.

‡ Only developing testes could be counted until obscured by forming vitellaria. Numbers shown may be underestimates.

§ The size of the cirrus sac increases considerably in posteriormost proglottids of complete worms. Indicated size was probably affected by a few missing segments from 3 worms.

Table 2. Prevalence and mean intensity of *Bothriocephalus formosus* and *B. cuspidatus* infections in *Stizostedion vitreum* from Silver Lake, 1976–1979.

	Autumn (late Oct., Nov.)	Spring (April)	Summer (June–early Aug.)	Total
B. formosus				
Fish inf./exam. (%)	15/23 (65)	20/21 (95)	6/10 (60)	41/54 (76)
Worms (mean/exam. fish) max.	313 (13.6) 112	529 (25.2) 93	368 (36.8) 285	1,210 (22.4) 285
B. cuspidatus				
Fish inf./exam. (%)	5/23 (22)	12/21 (57)	0/10	17.54 (31)
Worms (mean/exam. fish) max.	62 (2.7) 47	415 (19.8) 120	0	477 (8.8) 120

spring collections; data were combined (Table 1). Summer worms were considerably shorter and measured structures were smaller. Meristic and morphometric features in 19 worms with complete strobilae were compared with the incomplete description of Mueller and Van Cleave (1932), as well as with measured samples of their cotypes (Table 1). Available museum specimens of *B. formosus* and *B. claviceps* were also examined for verification of identity.

Seasonality

Prevalence and intensity of infection were considerably higher for *B. formosus* (76%, 22.4) than for *B. cuspidatus* (31%, 8.8) (Table 2). Walleye were most frequently and heavily infected with *B. formosus* during summer and with *B. cuspidatus* during spring (Table 2). Summer infections with *B. formosus* were influenced by 1 heavily infected fish that had 285 worms.

Table 3. Seasonal development of *Bothriocephalus formosus* and *B. cuspidatus* in *Stizostedion vitreum* from Silver Lake, 1976–1979.

Cestode developmental stages	No. of worms	Number and prevalence (%) of worms: Autumn (late Oct., Nov.)	Spring (April)	Summer (June–early Aug.)
B. formosus				
All stages	1,210	313	529	368
Juvenile (%)*	973	293 (94)	432 (82)	248 (67)
Mature (%)	184	8 (2)	88 (17)	88 (24)
Gravid (%)	53	12 (4)	9 (2)	32 (9)
B. cuspidatus				
All stages	477	62	415	0
Juvenile (%)	335	0 (0)	355 (86)	0 (0)
Mature (%)	93	41 (66)	52 (13)	0 (0)
Gravid (%)	29	21 (34)	8 (2)	0 (0)

* The percent prevalence compares data in vertical columns.

Walleye harbored juvenile and gravid *B. formosus* during all seasons; most worms recovered during autumn were juveniles (94%), and the highest proportion of mature and gravid adults (33%) was obtained during the summer (Table 3). No *B. cuspidatus* were found in walleye during summer; most spring worms were juveniles (86%), and all autumn worms were mature (66%) or gravid (34%) adults (Table 3).

Host relations

Parameters of *B. formosus* and *B. cuspidatus* infections were not affected by host sex. Prevalence and mean intensity of *B. formosus* infections were 79% and 19.0 in 28 male and 73% and 26.0 in 26 female walleye. *B. cuspidatus* infections were 36% and 9.1 and 30% and 8.5 in male and female walleye, respectively. No particular relationship between rates of infection and fish size was apparent; males and females were not significantly different in size.

Site of infection

Pyloric ceca of walleye appear to be the preferred sites of infection with both species of *Bothriocephalus,* particularly *B. cuspidatus,* during all seasons (Table 4). However, gravid worms occurred with similar frequency in both cecal and intestinal sites.

Infections in other hosts

The only adult *B. formosus* not collected from *S. vitreum* were 13 gravid worms from the pyloric ceca of 3 green sunfish, *Lepomis cyanellus,* captured in Tichigan Lake Canal during the summer of 1979. In addition, 13 larval *B. formosus* (Bf) and 9 larval *B. cuspidatus* (Bc) were found during the spring (20) and summer (2) of 1978 on the liver of 6 fishes, 1 *Pomoxis annularis* (1 Bc), 2 *S. vitreum* (3 Bf), 1 *Pomoxis nigromaculatus* (1 Bc), 1 *Micropterus salmoides* (11 Bf, 5

Table 4. Seasonal site selection of *Bothriocephalus formosus* and *B. cuspidatus* in *Stizostedion vitreum* from Silver Lake, 1976–1979.

Season	No. of worms	Percent of worms in intestinal regions (% of juveniles, adults, gravid worms)*				
		A	Ceca	B	C_1	C_2
B. formosus						
Autumn	313	5 (100, 0, 0)	59 (90, 5, 5)	32 (97, 0, 3)	4 (100, 0, 0)	0
spring	529	1 (83, 17, 0)	68 (76, 22, 2)	30 (95, 4, 1)	0.4 (50, 50, 0)	0.4 (100, 0, 0)
Summer	368	12 (66, 29, 5)†	50 (68, 25, 7)	37 (67, 20, 13)	1 (50, 0, 50)	0
B. cuspidatus						
Autumn	62	0	97 (0, 65, 35)	1.5 (0, 100, 0)	1.5 (0, 100, 0)	0
Spring	415	0	85 (86, 12, 2)	15 (84, 14, 2)	0	0

* Percent of worms in the stomach (A), ceca, small intestine (B), and first and second halves of large intestine (C_1 and C_2) (percent of juveniles with only immature segments if segmented, adults with sexually mature segments, adults with segments gravid with eggs).

† It is possible that regurgitation was a variable affecting this anterior localization of worms.

Bc) and 1 *Ambloplites rupestris* (1 Bc) from Silver Lake. Cestodes from walleye were 3–22 mm long and with 6–70 segments each. Those from other hosts were 2–9 mm long and with 2–35 segments each. The scolex was well defined in all juveniles.

Discussion

Morphometric and meristic features of *B. cuspidatus* were similar in shape and size to those originally described by Cooper (1917) and subsequent observers (Van Cleave and Mueller, 1934; Hugghins, 1972). Thus, morphometric analysis was not warranted. The smaller summer *B. formosus* from Wisconsin were similar to those in the original description (Table 1). Mueller and Van Cleave's (1932) specimens were collected during the summer. Therefore, their description of *B. formosus* does not express the full range of variation exhibited by *B. formosus* in this study (Table 1). The scolex of *B. formosus* from Wisconsin agrees with the text description of Mueller and Van Cleave (1932). However, the scolex of Oneida Lake cestodes (Mueller and Van Cleave, 1932, fig. 20) was markedly smaller (Table 1) and its anterior tip was more dome-shaped. The dome-shaped scolex tip of the 6 cotypes (USNM Helm. Coll. No. 8690) (Table 1) was barely to moderately pronounced. Observed scolex differences are not considered sufficient to warrant considering Wisconsin material as a new species. Proglottids of the Wisconsin material were similar to those in the original description known only from summer material.

Reference specimens made available for study included *B. formosus* cotypes collected by J. F. Mueller in 1932 from *Percopsis omiscomaycus* in Oneida Lake (USNM Helm. Coll No. 8690) and *B. formosus* from *Etheostoma nigrum* in Chippewa County, Wisconsin (USNM Helm. Coll. No. 78221), which were identical to my material. Misidentifications included "*B. formosus*" from *E. nigrum* in Ingram County, Michigan (USNM Helm. Coll. No. 76699) and from *Pimephalus notatus* in Posey County, Indiana (HWML Coll. No. 21487), as well as "*B. claviceps*" (actually *B. formosus*) from *Lepomis cyanellus* in Keith County, Nebraska (HWML Coll. Nos. 19827, 19893).

Summer *B. formosus* and their reproductive structures (except egg size) were considerably smaller compared to autumn–spring worms (Table 1). Number of proglottids/strobila was also considerably fewer, but percent of gravid segments was greater in summer (Table 1). Clearly these data represent a seasonal (temperature-related) growth-maturity phenomenon. Growth appears to proceed quickly during the autumn (early in the infection cycle) and large size is retained in the overwintering worms. In the summer, rapid maturation, perhaps of new recruits, leads to small size adults. Musselius (1962 *in* Davydov, 1978) reported that cestodes in fish intestines at water temperatures of 22–25°C mature and produce eggs almost twice as fast as at 16–19°C. It took *Bothriocephalus acheilognathi* Yamaguti, 1934, 12–14 and 22–25 days to attain sexual maturity at 22–25° and 15–18°C, respectively (Davydov, 1978). Granath and Esch (1983) noted that development of *B. acheilognathi* from North Carolina was stimulated by water temperature. Growth and fecundity of *B. acheilognathi* were also found by Davydov (1978) to be

dependent on worm size and affected by temperature. Moravec (1985) reported that gravid *B. claviceps* from Czechoslovakia were larger in May to July than in August. Robert et al. (1988) observed many large segments of *Bothriocephalus gregarius* from France during July compared to the fewer and smaller segments observed later in the season. Bona (1983) shed more light on this phenomenon with his careful biometrical study of the dilepidid cestode *Dendrouterina pilherodiae* Mahon, 1956. He analyzed differential rate of growth versus development and proposed a model showing how adult proglottids of different sizes can form. He concluded that growth assumes an S-shaped curve with an increasing, then a decreasing, rate. Wisconsin material also indicates that this growth-development phenomenon is additionally affected by host species. The 13 gravid *B. formosus* collected from *L. cyanellus* in Tichigan Lake Canal during the summer were similar in size to the larger autumn–spring worms obtained from walleye in Silver Lake (Table 1). This may represent an ecological phenomenon related to *L. cyanellus* becoming active and feeding on intermediate hosts earlier in the spring, or to its gut size. Riggs et al. (1987) also noted the relationship between size and fecundity of *B. acheilognathi* and cyprinid and poecilid fish host species and gut size in North Carolina. The absence of other collections from green sunfish from Wisconsin during other seasons does not allow further elaboration on that point.

Bothriocephalus cuspidatus is a common parasite of walleye (Van Cleave and Mueller, 1934; Hugghins, 1972; Deutsch, 1977; Sutherland and Holloway, 1979; Robinson and Jahn, 1980; and others). In land-locked Silver Lake, *B. cuspidatus* was far less common than *B. formosus* in walleye (Table 2). Neither species was found in 55 walleye examined from Tichigan Lake and its canal. Appropriate intermediate hosts are probably present in Tichigan Lake system as indicated by infection of *L. cyanellus* from the Tichigan Lake Canal. However, the vagile green sunfish might have picked up the infection elsewhere, e.g., the Fox River. Other helminth species also found to be more dominant in Silver Lake fishes compared to Tichigan Lake include *Proteocephalus ambloplitis* (Leidy, 1887) Benedict, 1900 (see Amin, 1990a; Amin and Cowen, 1990), caryophyllaeid cestodes (Amin, 1986a), and *Neoechinorhynchus* spp. (Amin, 1986b). The opposite trend was observed in *Pomphorhynchus bulbocolli* Linkins *in* Van Cleave, 1919 (see Amin, 1987) and similar infection parameters were noted for *Proteocephalus pinguis* La Rue, 1911, in both lakes (Amin, 1990b). Environmental pecularities and ecological variables, relating to differences in the life cycles of each of the parasitic groups, particularly the intermediate host, may account for the expression of the above patterns. Parasites using cyclopoid copepods are less represented in Tichigan than in Silver Lake.

The similar prevalence and intensity of both *B. formosus* and *B. cuspidatus* infections in male and female walleye of all sizes over 15 cm appear to reflect a relatively uniform level of infection in fish paratenic hosts since walleye become piscivorous at about 6–8 cm (Niemuth et al., 1972). No second intermediate host is necessary in the cycle of both species of cestodes. This pattern of infection with *Bothriocephalus* was previously noted by Essex (1928), Mitchell and Hoffman (1980), and others. In the present study, the stomachs of some larger walleye contained walleye and bluegill, *Lepomis macrochirus.* These prey fish may represent a link in the chain of walleye infection in Silver Lake. The increased prevalence of *Bothriocephalus* sp. in female yellow perch, *Perca flavescens,* in Ontario was apparently related to increased predation by older females which, unlike males, "showed an increase in food size . . . (crayfish and fish) . . . with increasing size . . ." (Cannon, 1973). Similar relationships between intensity of infection and host size were also reported for *B. claviceps* from perch, *Perca fluviatilis,* in Czechoslovakia (Scholz, 1986) and for *B. gregarius* from turbot, *Psetta maxima,* in France (Robert et al., 1988).

Of the 54 walleye examined from Silver Lake, 41 (76%) were infected with *B. formosus* and 17 (31%) with *B. cuspidatus* (Table 2). All 17 fish infected with *B. cuspidatus* were also concurrently infected with *B. formosus.* Both species occupied pyloric cecal sites (Table 4). Site selection, interspecific competition, and/or seasonality of intermediate hosts may have influenced the reproductive strategy of both cestode species in walleye. At the infrapopulation level, individual concurrently infected walleye with high intensity of *B. formosus* infections usually had light infections with *B. cuspidatus*; the opposite was true. *Bothriocephalus formosus* appears to be the dominant cestode species in Silver Lake walleye. Recruitment, maturation, and reproduction of *B. formosus* occur during all seasons (Tables 2, 3).

The major recruitment season appears to be autumn when 94% of cestodes were juveniles; partial generation overlap is indicated. Cestode buildup and maturation increased reaching a maximum intensity (36.8) (Table 2) and proportion of mature and gravid worms (33%) (Table 3) during summer when the highest proportion in nonpyloric cecal sites (37%) was noted (Table 4). No collections were made during winter. The seasonality of *B. formosus* has not been reported in any other location in North America, but comparable patterns were reported in other bothriocephalid cestodes, e.g., *B. claviceps* from eel (*Anguilla anguilla*) in Czechoslovakia (Moravec, 1985), *B. claviceps* from perch (*Perca fluviatilis*) in Czechoslovakia (Scholz, 1986), and *B. acheilognathi* from *Gambusia affinis* in North Carolina (Marcogliese and Esch, 1989).

The reproductive cycle of *B. cuspidatus* in Silver Lake may be related to its decreased competitive success compared to *B. formosus*. In summer, when *B. formosus* reached its peak abundance and reproductive activity, *B. cuspidatus* was absent. This absence might have been affected by sample size of walleye but not its sex or size, which were shown above to be unrelated to prevalence or intensity of infection. Peak reproductive activity of *B. cuspidatus* (100% mature and gravid worms) was evident in the autumn (Table 3). This is in contrast to evidence from other studies of *B. cuspidatus* in single infections, which suggests that the usual breeding season of *B. cuspidatus* is summer in its fish definitive hosts (Van Cleave and Mueller, 1934; Amin, 1975; and others). The seasonal displacement of *B. cuspidatus* and change in its reproductive cycle allowed temporal niche sharing in the pyloric ceca of the same host species. The possible involvement of the seasonal distribution of intermediate hosts, or other ecological variables, in this phenomenon is not known.

The recovery of juveniles of both species of *Bothriocephalus* from the liver of *P. annularis, P. nigromaculatus, S. vitreum, M. salmoides,* and *A. rupestris* contrasts with Essex's (1928) original contention about the role of small fish as a source of infection of the definitive fish host. Essex (1928) originally thought that *B. cuspidatus* could be transmitted from fish to fish if the prey fish was recently ingested and had an infected copepod in its stomach. The fact that walleye of the sizes examined in this study (15–45 cm) are piscivorous suggests that the above species of fish serve as paratenic hosts in Silver Lake. This is the first report of fish paratenic hosts for either species of *Bothriocephalus*. Other sites for paratenic infection have, however, been noted, e.g., *B. gregarius* metacestodes infected the intestine of goby (Robert et al., 1988).

Deposited Specimens

Bothriocephalus formosus: HWML Coll. Nos. 31701–31707 and USNM Helm. Coll. Nos. 81264–81268. *Bothriocephalus cuspidatus:* HWML Coll. Nos. 31708, 31709 and USNM Helm. Coll. Nos. 81269, 81270.

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Literature Cited

Amin, O. M. 1975. Intestinal helminths of some southeastern Wisconsin fishes. Proceedings of the Helminthological Society of Washington 42:43–46.

———. 1986a. Caryophyllaeidae (Cestoda) from lake fishes in Wisconsin with a description of *Isoglaridacris multivitellaria* sp. n. from *Erimyzon sucetta* (Catostomidae). Proceedings of the Helminthological Society of Washington 53:48–58.

———. 1986b. Acanthocephala from lake fishes in Wisconsin: host and seasonal distribution of species of the genus *Neoechinorhynchus* Hamann, 1892. Journal of Parasitology 72:111–118.

———. 1987. Acanthocephala from lake fishes in Wisconsin: ecology and host relationships of *Pomphorhynchus bulbocolli* (Pomphorhynchidae). Journal of Parasitology 73:278–289.

———. 1990a. Cestoda from lake fishes in Wisconsin: the ecology and pathology of *Proteocephalus ambloplitis* plerocercoids in their fish intermediate hosts. Journal of the Helminthological Society of Washington 57:113–119.

———. 1990b. Cestoda from lake fishes in Wisconsin: occurrence of *Proteocephalus* from *Esox* and other fish species. Journal of the Helminthological Society of Washington 57:132–139.

———**, and M. Cowen.** 1990. Cestoda from lake fishes in Wisconsin: the ecology of *Proteocephalus ambloplitis* and *Haplobothrium globuliforme* in bass and bowfin. Journal of the Helminthological Society of Washington 57:120–131.

Bona, F. V. 1983. Variability and growth of cestodes: premises to a biometric analysis. *Dendrouterina pilherodiae meridionalis* n. subsp., parasite of *Egretta alba* (Ciconiformes) in Argentina and redescription of the type of *D. pilherodiae* Mahon, 1956 (Cestoda, Dilepididae). Part I. Revista Di Parasitologia 44:279–297.

Cannon, L. R. G. 1973. Diet and intestinal helminths in a population of perch, *Perca flavescens*. Journal of Fish Biology 5:447–457.

Cooper, A. R. 1917. A morphological study of bothriocephalid cestodes from fishes. Journal of Parsitology 4:33–39.

Davydov, O. N. 1978. Growth, development and fecundity of *Bothriocephalus gowkongensis* (Jen, 1955), a cyprinid parasite. Hydrobiological Journal 14:60–66.

Deutsch, W. G. 1977. Fish parasites from the Susquehanna River in Pennsylvania, with new host records. Proceedings of the Pennsylvania Academy of Science 51:122–124.

Essex, H. E. 1928. On the life history of *Bothriocephalus cuspidatus* Cooper, 1917, a tapeworm of the wall-eyed pike. Transactions of the American Microscopical Society 47:348–355.

Fischthal, J. H. 1947. Parasites of northwest Wisconsin fishes. I. The 1944 survey. Transaction of the Wisconsin Academy of Sciences, Arts and Letters 37:157–220.

Granath, W. O., Jr., and G. W. Esch. 1983. Temperature and other factors that regulate the composition and infrapopulation densities of *Bothriocephalus acheilognathi* (Cestoda) in *Gambusia affinis* (Pisces). Journal of Parsitology 69:1116–1124.

Hoffman, G. L. 1967. Parasites of North American Freshwater Fishes. University of California Press, Berkeley and Los Angeles. 486 pp.

Hugghins, E. J. 1972. Parasites of fishes in South Dakota. South Dakota Experiment Station Bulletin 484:1–73.

Kuntz, S. M., and W. F. Font. 1984. Seasonal dynamics of *Allopodocotyle boleosomi* (Pearse, 1924) n. comb. (Digenea: Opecoelidae) in Wisconsin darters (Etheostomatinae). Canadian Journal of Zoology 62:2666–2672.

Marcogliese, D. J., and G. W. Esch. 1989. Alterations in seasonal dynamics of *Bothriocephalus acheilognathi* in a North Carolina cooling reservoir over a seven year period. Journal of Parasitology 75:378–382.

Mitchell, A. J., and G. L. Hoffman. 1980. Important tapeworms of North American freshwater fishes. United States Department of the Interior, Fish and Wildlife Service, Fish Disease Leaflet 59:1–18.

Moravec, F. 1985. Occurrence of endoparasitic helminths in eels (*Anguilla anguilla* L.) from the Macha Lake fishpond system, Czechoslovakia. Folia Parasitologica (Praha) 32:113–125.

Mueller, J. F., and H. J. Van Cleave. 1932. Parasites of Oneida Lake fishes. Part II. Descriptions of new species and some general taxonomic considerations, especially concerning the trematode family Heterophyidae. Roosevelt Wild Life Annals 3: 79–137.

Niemuth, W., W. Churchill, and T. Wirth. 1972. Walleye, Its Life History, Ecology, and Management. Publication No. 227-72, Department of Natural Resources, Madison, Wisconsin. 20 pp.

Riggs, M. R., A. D. Lemly, and G. W. Esch. 1987. The growth, biomass, and fecundity of *Bothriocephalus acheilognathi* in a North Carolina cooling reservoir. Journal of Parasitology 73:893–900.

Robert, F., F. Renaud, E. Mathieu, and C. Gabrion. 1988. Importance of the paratenic host in the biology of *Bothriocephalus gregarius* (Cestoda, Pseudophyllidea), a parasite of the turbot. International Journal for Parasitology 18:611–621.

Robinson, G. L., and L. A. Jahn. 1980. Some observations of fish parasites in pool 20, Mississippi River. Transactions of the American Microscopical Society 99:206–212.

Scholz, T. 1986. Observations on the ecology of five species of intestinal helminths in perch (*Perca fluviatilis*) from the Macha Lake fishpond system, Czechoslovakia. Věstnik Ceskoslovenski Společnoski Zoologicke, 50:300–320.

Sutherland, D. R., and H. L. Holloway, Jr. 1979. Parasites of fish from the Missouri, James, Sheyenne, and Wild Rice rivers in North Dakota. Proceedings of the Helminthological Society of Washington 46:128–134.

Van Cleave, H. J., and J. F. Mueller. 1934. Parasites of Oneida Lake fishes. Part III. A biological and ecological survey of the worm parasites. Roosevelt Wild Life Annals 3:161–334.